Chapter V. THEORETICAL CONSIDERATIONS.

1. FACTORS DETERMINING DISTRIBUTION.

As a result of our labors, the distribution patterns of a large number of species have been portrayed graphically. Even if these were offered merely as empirical facts, without any attempt at an explanation, we feel that their publication would be fully justified. But many of these distribution patterns are not purely empirical. On the contrary they stand in evident relation to certain physical factors in the environment. The nature of these factors has been already discussed rather fully in chapter II, and concrete examples of their influence upon distribution have been instanced repeatedly in chapter IV. The factors which we believe to be most effective directly and indirectly in determining the distribution of the bottom-dwelling species throughout these waters are (1) the character of the bottom, considered chiefly in relation to its physical texture; and (2) the temperature of the water. To these we may add another factor of far less extended application, so far as concerns our dredging results. This is (3) depth of water, or, perhaps, more strictly, proximity to shore, though this statement demands considerable explanation.

We are quite aware that several other factors are generally recognized[a] as being of importance in determining the distribution of marine organisms; and we do not wish to be understood as limiting these agencies to the ones here enumerated. But we are concerned at present only in explaining the phenomena encountered by us during our dredging operations in the vicinity of Woods Hole. The factor of salinity is doubtless of the highest importance in determining the fauna of salt marshes and estuaries, and even that of the open sea near the mouths of rivers.[b] But there are, within the limits of our region, no streams of sufficient magnitude to seriously affect the fauna at any considerable distance from shore. Among all the species taken in the course of our dredging, we have encountered not more than two or three which seemed to be restricted to the upper portions of Buzzards Bay, where alone the water was found to be diluted in any considerable degree (cf. charts 215-218). The most striking case of this sort was that of the sponge *Tethya gravida*, which, so far as we know, has only been taken near the head of Buzzards Bay.

The presence or absence of other organisms, which may serve as the food of a given species or which may furnish it with a necessary basis for attachment, is surely to be ranked as an important factor in influencing distribution. But these other organisms are, in turn, dependent upon inorganic factors, such as those which we have mentioned, and thus the latter may be regarded as ultimately responsible for the distribution in all cases.

[a] For admirable general discussions of this subject the reader is referred to C. G. J. Petersen (1893), Herdman et al. (1894), Walther (1894), and Allen (1899).

[b] Certain marine fishes have been held to be sensitive, directly or indirectly, to comparatively slight differences in the density of their surrounding medium. Petterssen (1894) has shown that the appearance of herring upon the Norwegian coast is correlated with periodic changes of water salinity; but since the latter changes are simultaneous with changes in the temperature and in the food supply, it would seem difficult to exclude the influence of these latter factors. On the contrary, it is well known (vide Sumner, 1906, p. 68) that many marine fishes are capable of living equally well in waters of widely different degrees of salinity.

2. THE LOCAL FAUNA AS INFLUENCED BY THE CHARACTER OF THE BOTTOM.

Of the three factors enumerated above, the first (character of bottom) is beyond doubt the most effective one in determining the distribution of organisms within the limits under consideration by us. It is a mere truism that solid objects are necessary for the attachment of whole groups of fixed organisms, e. g., hydroids, Bryozoa, ascidians, barnacles, etc., as well as of many algæ. The presence of stones or shells is therefore essential to the existence of such forms. The absence of a suitable basis of support we believe to account in the main for the comparative scarcity of hydroids in Buzzards Bay. Soft mud doubtless interferes, likewise, with the respiratory currents of many organisms, and these, too, would be better fitted to live in Vineyard Sound. Other forms, on the contrary, require a muddy bottom in which to burrow. Thus, many of our local annelids and certain bivalve mollusks are, for the most part, restricted to Buzzards Bay. In some cases, as stated above, the relation between fauna and bottom is less direct, as witness the small tube-dwelling worms of the genus *Spirorbis*, which commonly adhere to various algæ.

Since, as we have seen, Vineyard Sound and Buzzards Bay are rather sharply distinguished from each other by the presence or absence of mud on the one hand, and of clean sand and gravel on the other, it is natural that the most obvious distinction in distribution should be that between the predominantly Sound-dwelling species and the predominantly Bay-dwelling species. By reference to the lists of species contained in chapter III it will be found that 40 per cent of the more prevalent species dredged by the *Fish Hawk* in Buzzards Bay do not appear in the list of the more prevalent species dredged by the *Fish Hawk* in Vineyard Sound; while 35 per cent of the species contained in the latter list do not appear among the former. Our distribution charts, likewise, reveal the occurrence of many species which are restricted wholly or chiefly to Vineyard Sound, and a considerable number of others which are restricted wholly or chiefly to Buzzards Bay.

Furthermore, within each of these major bodies of water, the local distribution of many forms is very obviously determined by the presence of one or another variety of bottom. Thus it happens that many species whose occurrence in Vineyard Sound is general are found in Buzzards Bay only in the adlittoral zone, particularly along the Elizabeth Islands. Here the mud is less prevalent, and the bottom approximates in character much of that to be met with in Vineyard Sound. A type of distribution which is almost the converse of the last is met with in the case of certain mud-dwelling species, which are of general occurrence throughout the bottom of Buzzards Bay, but which in Vineyard Sound are confined to a few definite areas where mud is known to be present (e. g., *Yoldia limatula*, chart 135). Vineyard Sound is divisible, as has been already stated, into an eastern half, in which the bottom is predominantly gravelly and stony, and a western half, in which the bottom is mainly of sand (see chart 227). Accordingly, many species, particularly among the attached forms, are lacking in the western half of the Sound, except in the littoral and adlittoral zones; while certain sand-dwelling species (e. g., the "lady crab," *Ovalipes ocellatus*, and among fishes the rays and flounders) are especially prevalent in that very region. Such cases as these are not always easy to distinguish from those to be discussed presently, in which temperature determines which half of the Sound is inhabited by a given species. The lower end of Buzzards Bay, like its eastern shore, is comparatively free from deposits of mud, and accordingly we often meet with species here which occur in various parts of the Sound, but which are rarely or never met with in the more central parts of the Bay. Here again the temperature factor often leads to similar appearances, and it is therefore necessary to consider the total range of a species before we can form any definite conclusions as to which factor is responsible in a given case.

The scarcity or apparent total absence in Buzzards Bay of a considerable number of species belonging to each of the subkingdoms is, we believe, due chiefly if not entirely to the character of the bottom. It is true that the annual extremes of temperature are somewhat greater in the Bay than in the Sound, and it is true that the water density of the former is slightly lower; but we would attribute little importance to these factors in determining the differences in their respective faunas.

Tables presented in chapter III show that the list of prevalent species for the *Fish Hawk* stations in Buzzards Bay is almost identical with that for muddy bottoms; while the list of prevalent species for the *Fish Hawk* stations in Vineyard Sound includes but two species which were not contained either in the list for sandy or in that for gravelly bottoms. This, however, can hardly be regarded as *independent* evidence that the differences in fauna between the two bodies of water are due to differences of the bottom.

As regards the variety of life found to occur upon the various types of bottom, it was shown above that the number of species per dredge haul was greatest for the bottoms of gravel or stones and least for the sandy bottoms, while the muddy bottoms held an intermediate position in this respect. It was pointed out, however, that the greater wealth in species, recorded for the muddy bottoms, as compared with the sandy ones, might be due, in part at least, to the fact that the dredge cut more deeply into the former, and thus obtained a fairer representation of the burrowing organisms.

It was likewise shown statistically that the average number of species per dredge haul was greater in Buzzards Bay than in Vineyard Sound. This was true despite the fact that the total number of species encountered was much greater in the Sound than in the Bay. We have interpreted these facts as signifying that while the wealth of species is, on the average, as great or even greater at each particular point on the floor of Buzzards Bay, the greater diversity of conditions in Vineyard Sound as a whole results in its furnishing a habitat to a greater variety of species.[a] This conclusion is quite in harmony with the fact that the number of "prevalent" species for Buzzards Bay—i. e., the number of those taken at one-fourth or more of the dredging stations—is about the same (slightly greater, indeed) than the similar number for Vineyard Sound. On the assumption of a greater uniformity of life conditions throughout the former, a larger proportion of the Bay-dwelling species might be expected to occur at one-fourth or more of the stations, even though the total number of such species were smaller.

We think that the reader will be impressed, as are we, by the approximate agreement among the figures representing the wealth in species of the different types of bottom distinguished by us and of the different subdivisions of the area dredged. The figures (p. 77) denoting the average number of species per dredge haul range from 35.2 for the *Phalarope* stations in Vineyard Sound to 39.7 for the Crab Ledge stations, the mean for all the stations being 37.0. Again, the lists of more "prevalent" species for various

[a] See, however, discussion on pp. 79, 80, which renders this conclusion somewhat uncertain.

habitats and regions are of approximately equal length, the number of species ranging, with a single exception, between 50 and 55. These figures, of course, in no way express the relative *wealth of animal life* in these situations, this last being dependent upon the number of *individuals* rather than the number of species. Unfortunately we have no data sufficient for the purpose of giving a statistical expression to the real wealth of life upon different portions of the local sea floor. Particular spots were found, it is true, which were in large degree destitute of life, but whether or not any one of the types of bottom or of the larger subdivisions of our region was more densely populated than any other can not be stated with mathematical certainty. It is our general impression that living organisms were found to be somewhat less abundant upon bottoms of comparatively pure sand, although it is true that this is the prevailing type of bottom in the western portion of Vineyard Sound, to which many of our species are restricted.[a]

Another fact which may be regarded as surprising, despite the differences pointed out above, is the comparatively small proportion of the species which are restricted to any particular type of bottom. Thirty species are common to all three of the lists which give the prevalent forms for each type of bottom, this number representing, on the average, 60 per cent of the number contained in each list. But even this figure does not fairly express the number of those which were actually found with considerable frequency upon all three types of bottom, since each list is restricted to species so common as to have been encountered at one-fourth of a given group of stations. Again, only 26 per cent of the species contained in the list of prevalent mud-dwelling forms is peculiar to that list; while only 24 per cent of the list for bottoms of stones and gravel, and only 13 per cent of that for sandy bottoms are peculiar to their respective lists.

We do not think that these figures fairly express, however, the obvious differences in the characteristic faunal aggregations for different types of bottom, as presented to the eye. This is because they do not take into account the relative number of individuals belonging to the various species. Certain species which are characteristic of muddy bottoms (e. g., certain bivalve mollusks and worms) are present in great numbers in an average dredge haul made upon such a bottom. But along with them are smaller numbers of a great variety of species, which are not especially characteristic. The same may be said of the other types of bottom. Thus the real distinctness of the faunal aggregations in question could only be adequately expressed by reference to the relative abundance of each species.[b] Again it must be once more emphasized that the mixing up, in a single dredge haul, of organisms from several quite distinct bottoms is in some measure responsible for this apparent lack of distinctness in their respective habitats. This is particularly true of relatively small areas of sea floor, such as those under consideration, in which quite various deposits are found to alternate with one another at frequent intervals. It is likely, indeed, that under such circumstances there is much overlapping and intermingling of faunal aggregations which elsewhere might be far more distinct. Finally, it must be remembered that the lists of "prevalent" species, as here constituted, exclude many forms which are highly characteristic of the bottoms in question, and which, in some cases, are restricted to them.

[a] It is here, indeed, that line fishing for mackerel and flounders is carried on with the greatest success.

[b] Of course, in a certain measure the wealth of a given species in individuals determines the frequency with which it appears in the dredging records. It is self-evident that the more abundant species are more likely to be taken than less common ones.

It would be hard to characterize in any brief statement the faunal assemblages proper to the various types of bottom. Such assemblages have been presented in four illustrative cases (p. 58–62), and composite pictures, including the more characteristic species, have been given elsewhere in chapter III. An attempt to still further condense these data would, we fear, result in a mere statement of platitudes. It may be allowable to mention, however, that the most characteristic species found upon muddy bottoms were annelids and bivalve mollusks, many of which were restricted to such bottoms; the most characteristic species found upon bottoms of stones or gravel were hydroids, Bryozoa, and ascidians; while the few species which were in any real sense restricted to bottoms of clear sand were either burrowing species (*Ovalipes*, *Echinarachnius*, certain lamellibranchs), or fishes (flounders and skates) which adhered closely to the bottom.

3. THE INFLUENCE OF TEMPERATURE.

The temperature factor is, with little doubt, the controlling one in the case of many species belonging to several different phyla. On page 74 is given a list of species which were dredged predominantly or exclusively in the colder waters of the region, i. e., at the western end of Vineyard Sound and the mouth of Buzzards Bay. Here the summer temperature of the bottom water averages about 10° F. (5.6° C.) lower than in the immediate neighborhood of Woods Hole. Reference to the stated ranges of these species revealed the fact that in 15 out of the 20 cases they are predominantly northward-ranging forms, some of which, indeed, are near their southern limit of distribution. Reference has also been made to a number of less common forms having a similar distribution, but which are not included among those for which distribution charts have been prepared. This large proportion of northward-ranging species among those occupying the colder waters of Vineyard Sound and Buzzards Bay is significant in view of the fact that a decided minority (23 per cent) of the species dredged by us with any frequency throughout the region at large are to be classed as northward-ranging, according to the standard employed.

It is of interest, also, to note that a large proportion of these colder water species were likewise taken by us at Crab Ledge, off Chatham, where the water temperatures in summer are even lower than at the mouth of Vineyard Sound. At Crab Ledge and at certain other outlying points were also taken a considerable number of species which appear never to enter Vineyard Sound or Buzzards Bay at all. So far as we have ascertained the ranges of the species, they belong, almost without exception, to the "Acadian" fauna characteristic of the waters north of Cape Cod.

Another list was presented (p. 76) of species which, though otherwise of general distribution throughout Vineyard Sound, and in many cases throughout Buzzards Bay as well, are absent from just those waters to which the northern types are restricted. This list was found to include none of the strictly northern types, while more than half of the species there included were forms which found in Cape Cod their northern limit of distribution. It is probable that the temperature factor is the one responsible for this type of distribution in some cases at least. Many of these species, it is significant to state, are conspicuously absent from Crab Ledge. On the other hand, it is likely that for some other organisms (e. g., the ascidians) the uniformly sandy condition of the bottom in this outer portion of Vineyard Sound and the scarcity of solid objects suitable for attachment render it an unfavorable habitat.

Although we believe these evidences of the distribution of local species with relation to temperature to be well-nigh conclusive, the fact must be admitted that there occur in Vineyard Sound and Buzzards Bay a considerable number of predominantly northward-ranging species, and a yet greater number of southward-ranging ones, whose distribution within local waters bears no possible relation to temperature. These are in some cases of very general occurrence; in others their distribution appears to be determined by the character of the bottom.

The actual mode of operation of temperature in restricting the distribution of species locally is not easy to state, and it is probable that no single formula is applicable to all cases. In chapter II the temperature conditions throughout local waters have been discussed rather fully. It has been shown that the temperature of those portions of Vineyard Sound and Buzzards Bay which immediately join the ocean is lower than that of the more inclosed waters for probably not more than half of the year, the difference being greatest during the summer months. It was also shown to be probable that all the waters of the region reach a point not far from the freezing point of salt water for a longer or shorter period during the winter. In the light of what we know regarding local temperature conditions on the one hand and the distribution of our marine fauna on the other, it will be of interest to consider certain theories which have been put forward to explain the part played by this factor in limiting the distribution of organisms in general.

The influence of temperature in determining the distribution of marine animals was emphasized by Forbes and by Dana more than 50 years ago, and has been accepted as almost self-evident by a large number of naturalists. Just how this factor operates in limiting the distribution of a given species is, however, far from plain. Dana,[a] in 1852, introduced the concept of "isocrymal lines," or lines showing the mean temperature of the waters along their course for the coldest 30 consecutive days of the year. Ordinary isotherms, or lines of mean annual temperature, he rejects as inadequate, on the ground that "the cause which limits the distribution of species northward or southward from the Equator is the cold of winter rather than the heat of summer or even the mean temperature of the year" (p. 1452).

Such a principle certainly does not explain the effect of temperature upon distribution within the limits of our local waters. Here the minimum winter temperatures are probably nearly the same throughout the entire region. If there are any local differences of regular occurrence, it is without doubt the shallower, more inclosed waters which attain the lowest winter temperatures. But these are precisely not the ones which are occupied by the northern forms of which we have spoken. Within local waters it is certainly the summer temperatures rather than the winter ones which are chiefly effective in limiting the distribution of species.

Verrill (1866, p. 249) maintained that for birds "the essential limiting cause is the average temperature of the breeding season, which for the majority of our birds may be taken as April, May, and June." This idea was apparently suggested by the conclusions of certain botanists respecting the distribution of plants. Merriam (1895, 1898), following out the same thought, has been led to the belief that "[land] animals and plants are restricted in northward distribution by the total quantity of heat during

[a] Dana, 1852, p. 1451–1592; 1853, p. 153–167, 317–327.

the season of growth and reproduction" (1895, p. 233); while "animals and plants are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year" (p. 234). The phrase "total quantity of heat" above employed is not to be taken in a strict sense, however, but implies "the effective temperatures or degrees of normal mean daily heat in excess of this minimum [6° C.]" which "have been added together for each station, beginning when the normal mean daily temperature rises higher than 6° C. in spring and continuing until it falls to the same point at the end of the season" (p. 232–233). "In conformity with the usage of botanists, a minimum temperature of 6° C. (43° F.) has been assumed as marking the inception of the period of physiological activity in plants and of reproductive activity in animals" (p. 232).

It is obviously impossible without qualification to apply this principle in explaining the distribution of marine animals. Many of these, as is well known, breed during the coldest months of the year, at a time when the temperature lies considerably below that assumed by Merriam as a necessary minimum for physiological activity; and there is no general agreement in the breeding season of even closely related forms. Unfortunately, the period of sexual reproduction is not definitely known for the vast majority of our local species. The greater part of such definite observations as are available are contained in the rather meager notes of Bumpus (1898, 1898a, 1898b), Mead (1898), and Thompson (1899), which cover only the spring and summer months. For a few species, however (e. g., certain amphipods [a] and the mollusk *Littorina palliata*), we have definite evidence that eggs are laid nearly or quite throughout the year.

From the data offered by Garstang (1894) for the breeding periods of marine animals at Plymouth, England, we may make a rough computation of the percentage of the species which breed during each month of the year in those waters. The following table, based upon records for about 200 species, presents these figures:

	Per cent.		Per cent.
January	14	July	23
February	20	August	21
March	23	September	16
April	29	October	9
May	33	November	7
June	28	December	5

It is impossible to state how far these figures are representative of the total marine fauna, even at Plymouth, and how far they have depended upon the relative activity of the observers during different months, but they seem to show that a considerable proportion of the species reproduce during the coldest months of the year.[b] And it would be a safe assumption, even in the absence of such confirmatory evidence as we possess, that the same statement would hold for the region of Woods Hole.

Before the operation of Merriam's law can be accepted as a sufficient explanation of the non-occurrence of certain southern species in the colder waters of this region, it must be shown that the "season of growth and reproduction" coincides with the period during which these waters are colder. As a matter of fact, we know that a considerable

[a] One of these, *Calliopius læviusculus*, is included in the list of the cold-water, northward-ranging species, which are, in our dredging records, restricted to the western part of Vineyard Sound.

[b] It must be added, however, that the waters in the neighborhood of Plymouth never reach such low temperatures as are recorded during the winter months for Vineyard Sound and Buzzards Bay. (See p. 183, 184, below.)

number of species belonging to this category (though not these in particular) do reproduce sexually during the summer months. In few cases, if any, however, do we know from local observations that their sexual period is confined to these months. We may comment parenthetically upon the urgent need of determining the reproductive condition of local marine organisms throughout the entire year.[a]

In the case of one species among those which appear to be restricted to the warmer waters of the region we have definite evidence that an actual destruction of adult organisms may occur as a result of extreme cold in winter. We refer to the common sea urchin, *Arbacia punctulata*, which, as our records show (see pp. 114, 115), was almost exterminated in Vineyard Sound during the winter of 1903–4. And it is well known to fishermen and others that great numbers of dead fishes and mollusks of certain species are frequently found after a particularly hard spell of cold weather.[b] This is sometimes attributed to the action of "anchor ice" or "ground frost." Gould (1840) cites the case of an extensive destruction of oysters which was believed to be due to this agency. That anchor ice does form in salt water, even at the depth of a number of fathoms, and that it may "freeze around fish caught in nets," is vouched for by Sir William Dawson and others.[c] On the other hand, we are informed by Prof. Herdman that he has had personal knowledge of the death from cold of fishes in aquaria, and even of burrowing mollusks along shore, in cases where actual freezing was out of question. It seems difficult, indeed, to believe in such a wholesale formation of anchor ice throughout Vineyard Sound as would be necessary to account for the extermination of the sea urchins by this agency. However, the extermination did occur during an exceptionally cold winter, and it seems a legitimate inference that it resulted in some way from the cold.

Now it is known that *Arbacia* finds in this region its northern limit of distribution upon our coast. It would seem, therefore, that in this latitude it is adapted to withstanding the average winter but not the exceptional one. On the other hand, no mere reference to *winter* temperatures can explain the absence of this species from the western end of Vineyard Sound, or from Crab Ledge. For, although at these latter points the summer temperatures are considerably lower than they are nearer Woods Hole, the winter temperatures are no lower, and possibly, indeed, not so low. Here, then, the law of Merriam may have application. *Arbacia* may not be adapted to reproducing in these colder waters.

But Merriam's principle, in its completed form, really contains two wholly distinct principles. The second is that animals are "restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year" (1895, p. 234). It is not stated whether this effect has to do with the ability of the adult organism itself to withstand higher temperatures, or whether the reproductive power is curtailed.

As regards the distribution of our local marine fauna, this phase of Merriam's law can apply, if at all, only to those predominantly northern species which were found to be restricted to the waters which were cooler during the summer months. And it does seem likely, indeed, that some of these species are unable to endure the high temperatures

[a] Aside from the case of certain fishes, our data for the winter months are derived almost wholly from an examination of tow-net collections made by Mr. Edwards.

[b] The scraping action of ordinary floating ice in removing the rock-weeds (*Fucus* and *Ascophyllum*) from the boulders along shore is pointed out in the botanical section of this report. This same agency doubtless restricts the distribution of such littoral animals as inhabit these weeds, and may even affect certain other forms, e. g., barnacles, which occur directly on the rocks. But it can, of course, have no influence upon the benthos, with which we are especially concerned here.

[c] Cf. Barnes, 1906, p. 210, 223–225.

attained by our more inclosed waters during the hottest part of the summer. For the great majority of cases, it must be admitted that this explanation is wholly conjectural. We know of at least one species of animal, however, which occurs in an active condition throughout Vineyard Sound during the winter and spring, but which, in these waters, passes into a condition of æstivation during the summer. This is the hydroid *Tubularia couthouyi* (see p. 565). Now it is of significance that in the colder waters at Crab Ledge, and beyond Marthas Vineyard, at a depth of 29 fathoms, active hydranths of this species have been dredged by us in July and August. Certain others among our local hydroids are likewise known to be dormant, or at least less active during the summer months. It is quite conceivable that at somewhat higher temperatures such species would be destroyed altogether.

We may say, then, that while there is some evidence for the operation of the principle of Merriam, in both of its phases, in determining the distribution of marine organisms in local waters, it seems likely that no single formula will suffice to explain all the phenomena involved;[a] and it is certain that we can form no adequate explanation of these until vastly more data are at hand. Both observation and experiment are demanded.

4. THE INFLUENCE OF DEPTH.

The great majority of species which were dredged by us in Vineyard Sound and Buzzards Bay were found to have a distribution, in local waters, which plainly bore no relation to depth. There are notable exceptions to this statement, however, some of which it is our purpose to discuss in the present section.

Leaving out of account the multitude of strictly "littoral" or intertidal forms, we meet with a considerable number of species which are limited to comparatively shallow waters. An analysis or the depth records for all these species[b] reveals the occurrence of many which were taken by us nearly or quite exclusively in waters less than 10 fathoms deep. Many of these species, indeed, occur wholly or predominantly at depths of less than 5 fathoms. A considerable number of such instances have been mentioned in the discussions for the separate subdivisions of the animal kingdom. A few of the commoner species, among those dredged, which show a distinct preference for the shallower waters, both in the Bay and the Sound, are: *Pista palmata*, *P. intermedia*, *Amphithoë rubricata*, *Bittium nigrum*, *Cerithiopsis emersonii*, *Crepidula convexa*, *Lacuna puteola*, *Lyonsia hyalina*, and *Mya arenaria*. Now, an examination of the distribution charts for these species shows that they were dredged chiefly, if not wholly, near shore. Some of them, at least, are known to inhabit the intertidal zone as well. It is a noteworthy fact fact that in some cases these species were dredged by the *Fish Hawk*, as well as by the *Phalarope*, but only at such of the *Fish Hawk* stations as were situated in the neighborhood of land. The depth at these points was often considerable, however (10 to 15 fathoms). Facts of this nature point to the conclusion that *proximity to shore* rather than *depth*, as such, may be the factor concerned in determining the lower limit of distribution for species of this sort. Before deciding the point definitely, it would be necessary to determine whether these "adlittoral" species occurred likewise on shoals at considerable distances from the land. Unfortunately, we have no satisfactory data on this subject,

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[a] Petersen (1893, p. 445), declares the view of Semper that "every single species is affected by the temperature in a way characteristic to itself alone is, I think, in the highest degree applicable to our marine animals."

[b] Tables presenting these data were prepared for use in the preparation of this report, but they have not been included herewith.

since the only shoal so situated (the Middle Ground), lying within the territory dredged by us, is made up to a considerable degree of shifting sand, ill adapted to the support of most animal life.

It may be well at this point to recall the type of distribution displayed by many species whose occurrence is general in Vineyard Sound, but which in Buzzards Bay are limited to the immediate vicinity of shore. If we had the data for the Bay alone at our disposal, it would be natural to suppose that the species had a definite bathymetric limit. We have, however, the best reasons for believing that it is the muddy character of the bottom, throughout the deeper parts of the Bay, which restricts the distribution of such forms.

Whatever be the causes which are responsible for limiting certain species to the shallower waters skirting the shore, it is certainly desirable that we should have a suitable word by which to designate both the fauna inhabiting these waters and the habitat which they occupy. For this purpose we have already employed at various times the term "adlittoral," which, so far as we know, has not been used by previous writers. Were there any unanimity, even among zoologists, in the use of the word "littoral" itself we should have no hesitation in recommending this term adlittoral. But the former word has been applied with very different degrees of inclusiveness, having been restricted by some to the intertidal zone; while by others it has been so extended as to take in the whole continental shelf.[a] It is in the more restricted sense that the term has been employed in the present report. For this, the word "tidal"[b] would be unequivocal and, indeed, self-explanatory. But, unfortunately, we could not well speak of a "tidal species," however appropriate the expression "tidal zone" would seem. Again, this word does not lend itself readily to a combination with Latin prefixes such as "sub" and "ad."

Now the word "sublittoral" has likewise been used with very varying inclusiveness,[c] from "just below the shore line" (Standard Dictionary) to a zone reaching to the greatest depths at which algæ flourish (Kjellman).[d] This latitude of definition rests upon the inherent ambiguity of the word itself. For there is nothing in its composition to imply a limit of depth, any more than there is in the words "submarine" or "subterranean."

It is therefore with hesitation that we have chosen the term "adlittoral" as designating the zone of shallow water immediately adjacent to the shore. We have not, it is true, set any definite lower limit of depth to this zone. That would doubtless vary with different species; likewise with the abruptness of descent of the sea floor.[e] But even in this loose and inexact sense it is certainly a convenient term by which to designate such waters as those dredged by us with the *Phalarope* and *Blue Wing*. As a useful alternative term "infratidal" might be employed, though there is no implication in this word of a lower limit of depth any more than in "sublittoral."

A converse type of distribution to that just discussed is exhibited by certain other forms which were dredged predominantly at depths of 10 fathoms or more. A few of the commoner of such species are: *Tubularia couthouyi*, *Strongylocentrotus droebachi-*

[a] E. g., by Petersen and by Ortmann. The littoral zone of Edward Forbes, on the other hand, extended from high-water mark to a depth of 2 fathoms. To make confusion worse confounded, we have the "littoral" fauna and flora of land zoology and botany, which are not marine at all.

[b] The substitution of this term is favored by Dr. Stejneger in a letter to one of the authors.

[c] A circular letter of inquiry which we sent to eight leading American ecologists revealed a surprising lack of unanimity in the use of all these terms.

[d] It is in this latter sense that the term is employed in the botanical section of this report (cf. p. 453, 454).

[e] Perhaps it would ordinarily be limited, in Buzzards Bay and Vineyard Sound, by the 5-fathom line, but this would not always be true.

ensis, *Cancer borealis*, *Ovalipes ocellatus*, *Pagurus acadianus*, *Astarte castanea*, *Astarte undata*, *Venericardia borealis*, and *Amaroucium stellatum*. Now, a number of the foregoing species, and in general a considerable proportion of those species which are limited to the deeper waters, have already been mentioned among the northern forms whose distribution is determined locally by temperature conditions. It must be repeated, however (see p. 28), that the waters of the western end of Vineyard Sound are little if any deeper on the average than those in the vicinity of Nobska and West Chop. The preference of these species for deeper waters is shown by their scarcity in the adlittoral zone. Certain of them, indeed, were dredged only by the *Fish Hawk*. It is more than likely that the somewhat lower summer temperature of these bottom waters, as compared with those skirting the shore, is the factor responsible for the restriction of some species to the former. The temperature factor is not the one directly concerned, however, in the case of all of the animals named. The distribution of *Ovalipes*, for example, is probably wholly determined by the character of the bottom. It is indeed known to occur on sand flats in shallow, warm water. The case of *Amaroucium stellatum* is interesting, since, although a deep-water species in the sense here employed, it is for the most part restricted to the more easterly portions of the Sound, where the bottoms are gravelly or stony. Thus its preference for deeper waters does not appear to be related to the temperature factor, though this is not entirely certain, since the deeper waters are everywhere somewhat cooler in summer than are the shoaler ones. The marked restriction of this species to the former is in striking contrast to the condition shown by the related *Amaroucium pellucidum constellatum* (= *A. constellatum* Verrill), which, although associated with *A. stellatum* at various points, is likewise found in profusion in shallow waters and even upon piles.

The vertical distribution of marine organisms is commonly designated by the term "bathymetric," and it has been sometimes supposed that depth was one of the primary factors determining distribution. There are, of course, at least four factors bound up in this one, viz, pressure, temperature, light, and gas content. Now, it is not at all certain to what degree, if any, pressure influences distribution. For the limited depths within our region, we may certainly leave it out of account.

Temperature is, as we have seen, definitely correlated with depth in the sea, just as it is with altitude on land. But there is, in local waters, little difference between surface and bottom temperature, except in those portions of the Sound and the Bay which adjoin the open ocean. Some of the cold-water species inhabiting these last are, as just stated, restricted to the greater depths. On the other hand, the restriction of certain species (see above) to the shallow water immediately skirting the shore may be due in some cases to the palpably higher temperature commonly met with at such points during the summer.

The relation of light to depth has been treated at some length in the botanical section of this report (p. 447–449), to which the reader is referred. It is likely that for relatively slight depths, such as those we are considering, the light factor has little direct effect upon the bathymetric distribution of animals. Indirectly it may be of influence in the case of certain forms which dwell upon algæ, and it is possible that some of the adlittoral species which have been discussed above are limited in this way.

It may be repeated in conclusion, however, that, as regards the species taken during our dredging operations, the great majority show little or no evidence of bathymetric distribution.

5. POSITION OF THE LOCAL FAUNA IN ZOOGEOGRAPHY.

Certain questions will naturally present themselves to the student of geographical distribution: What is the position of the Woods Hole fauna in the fauna of our American coast? To which of the larger zoogeographical regions does it belong? And is it situated in the middle of that region or close to one of its limits? In other words, do the majority of species have a range which extends mainly to the northward along this coast, or do the majority have, on the whole, a southward range; or is there no appreciable preponderance of one sort over the other? Simple as these questions may seem, it is difficult to give them an answer that is at all satisfactory. The known range, as distinguished from the actual range, of a species, is very frequently determined by historical accident. Thus the Bay of Fundy, Massachusetts Bay, Woods Hole, Newport, New Haven, Charleston, etc., frequently figure in our literature as limits of distribution, and this for reasons which are obvious to anyone familiar with the history of American marine zoology. Verrill and Smith, in their Vineyard Sound report, give Cape Cod as the southern limit, or the northern limit, of distribution for many species whose known range has since been extended far beyond this point.

Likewise the impossibility must be borne in mind of forming a just estimate of the geographical range of a species from any mere statement, however correct in itself, of the extreme limits of its distribution. The bathymetric range and other factors of its habitat at various latidudes must be taken into consideration. It was long ago pointed out by Edward Forbes (1844, p. 323) that "parallels in depth are equivalent to parallels in latitude." Walther (1894) states that from the surface down the temperature declines about 1° C. for each 18 meters. Accordingly, a species which is truly "boreal" in its general tendencies, and which occurs in abundance along the littoral zone, in northern latitudes, may none the less be found in the deeper colder waters of a region far to the southward. To state such a range merely in terms of latitude would be highly misleading. Again, it is obvious that the same importance must not be attributed to the isolated and occasional occurrence of a given species as to its occurrence at points where it is widespread and abundant. But in many of the tables which are available for consultation no distinction is made between the two.

Furthermore, the question as to the position of the Woods Hole fauna, from the standpoint of zoogeography, can not be answered until we have made clear what is to be understood by the "Woods Hole fauna." If by this expression we are to mean the aggregate number of species which have ever been taken within the limits adopted, the question would be a difficult one to answer, and the answer, when given, would be of little value. Such an inclusive list (which would be coextensive with our own annotated list or catalogue) would comprise not only the truly indigenous species, characteristic of the region, but the occasional stragglers borne from southern waters by the Gulf Stream, and likewise those northern forms which we have met with only at Crab Ledge or in the colder waters off Gay Head. These are mostly rare species locally, and are in no sense characteristic of the shallower waters of this section of the New England coast, yet the total number of such species is very considerable. In practice, however, it is difficult to separate the truly indigenous types from those which are to be regarded as exotics or stragglers. An arbitrary basis of selection must therefore be adopted. For the purposes of the ensuing analysis we have included as representative local species only those which have been taken at 10 or more of the dredging stations. There are thus eliminated a large number of forms which are relatively uncommon in these waters. The remaining ones, on the other hand, being, for the most part, of comparatively common occurrence, are just those whose general range of distribution is probably known with the greatest accuracy. Such a list, of course, comprises only bottom-dwelling organisms which occur at depths sufficiently great to be taken by the dredge. It consequently excludes the littoral and pelagic life as a whole, and therefore does not represent every element of the fauna.

Before entering upon such an analysis, however, it may be of interest to consider some of the prevalent opinions regarding the distribution of marine animals and plants upon this section of the coast.

It has been pretty generally assumed that Cape Cod forms a rather definite boundary between the fauna and flora inhabiting the regions above and below it. This was urged by Gould as early as 1840 (see Gould, 1840, p. 491), as the result of a study of the distribution of marine mollusks. Gould asserts that "many whole genera do not pass from one side to the other of this limit. Of the 203 marine species, 81 do not pass to the south and 30 have not been found to the north of the Cape, though many of them approach within a very few miles of each other." It was the opinion of Dana, likewise (1852, 1853), that there occurred at Cape Cod "a remarkable transition in species, and a natural boundary between the south and the north." Dana recognized four zoogeographical divisions of the Atlantic coast of North America, viz, the Acadian (first called by him "Nova Scotian"), Virginian, Carolinian, and Floridan. Cape Cod, he believed, served to divide the Acadian, lying to its north, from the Virginian on the south. Packard sought to distinguish another region, the "Syrtesian," on the north of the Acadian, between the latter and the arctic or polar.[a]

From a consideration of the actinians and echinoderms, in particular, Verrill (1866) was led to the belief "that there are portions of three distinct Faunæ to be distinguished on the coast of New England, viz: First, that known as the Virginian Fauna, extending from Cape Hatteras to the southern side of Cape Cod. * * * Second, that known as the Acadian or Nova Scotian Fauna, which extends along the shore from Cape Cod to the mouth of the St. Lawrence River, and includes * * * and many of the banks to the southward of Cape Cod, such as Nantucket Shoals; and perhaps the extreme end of Long Island. * * * Off the coast of New Jersey, also, there are deep-lying banks or shoals, which may be referred to this Fauna. * * * Third, a more arctic Fauna characterizes the eastern coast of Labrador and Newfoundland, and the Grand Banks, which extends far southward along our coast in deep water, influenced by the polar current of cold water[b] which skirts the northern part of our coast." This is the "Syrtesian" fauna of Packard.

Later (1871), referring especially to his dredging operations in Vineyard Sound and vicinity, Verrill writes: "One of the most important of the results of these investigations * * * is that while the shores and shallow waters of the bays and sounds, as far as Cape Cod, are occupied chiefly by southern forms, or the Virginian fauna,[c] the deeper channels and the central parts of Long Island Sound, as far as Stonington, Conn., are inhabited almost exclusively by northern forms, or an extension of the Acadian Fauna."

[a] Gill, 1873, p. 782, likewise recognizes the Arctic, Syrtesian, Acadian, Virginian, and Carolinian faunas.

[b] Concerning the probability of the existence of such a current, see Chapter II of the present report.

[c] Perkins, on the other hand, from a consideration of the mollusks of the vicinity of New Haven, wrote in 1869: "The fauna of the region belongs about equally to the Acadian and Virginian faunæ.

S. I. Smith (1879), likewise, from a study of certain groups of Crustacea, was led to believe that "the fauna from Cape Cod to Labrador is essentially a continuous one, or at least that there are no changes in it comparable with the differences between the fauna south and that north of Cape Cod Bay."

By the botanists, also, an equally great importance has been attributed to Cape Cod as a division between the floral regions distinguished by them. Harvey (1852) recognized one region north of Cape Cod, "extending probably to Greenland," while his second region extended from Cape Cod to the southward as far as Cape Hatteras.

Farlow wrote in 1882:

> It will be seen that Cape Cod is the dividing line between a marked northern and southern flora. In fact the difference between the floræ of Massachusetts Bay and Buzzards Bay, which are only a few miles apart, is greater than the difference between those of Massachusetts Bay and the Bay of Fundy or between those of Nantucket and Norfolk.

Somewhat earlier (1873), in answer to the question "whether northern species do not occur at exposed southern points, as Gay Head and Montauk, and southern species wander northward to Cape Ann," he gave the answer: "Most decidedly, I think, such is not the case." Such an extreme position as this has not, however, been taken by the author of the botanical section of the present report.

It would be futile, on the basis of our own researches into the fauna of the Woods Hole region, to enter into any extended discussion regarding the position of this region upon the zoogeographical map of the world.[a] As an adequate preliminary to such a discussion one would need to have a more or less intimate knowledge of the fauna of both shores of the Atlantic from the Arctic Ocean to the Tropics.

In a table in chapter III (p. 88,89) we have indicated the number of species, representing each of the chief subdivisions of the animal kingdom, which have been recorded from the Woods Hole region and from several other localities where a careful inventory of the fauna has been made. The number of species has been stated, also, which are known to be common to Woods Hole and to eastern Canada, and the number common to Woods Hole and to Plymouth. It will be found that 365(+4?) species are common to the Woods Hole and the Canadian lists. This number represents more than 30 per cent of the total number of determined Woods Hole species belonging to groups which were considered in making the Canadian list (i. e., omitting vertebrates and parasitic worms). On the other hand, only 15 per cent of the determined Woods Hole species (belonging to groups for which a comparison is possible) are common to the Plymouth list. A critical comparison of American and European species, and particularly an exhaustive search of the synonymy, would probably increase the latter figure somewhat.

It is much to be regretted that no list has been prepared with similar care of the fauna of some region lying about as far to the south of Woods Hole as the Gulf of St. Lawrence lies to the north. It might be confidently predicted that the percentage of our local species which would appear in such a list would be very greatly in excess of the 30 per cent which are common to Canada. Data bearing upon this phase of the subject will, however, be introduced presently.

One might perhaps have expected to find a much larger proportion of our Woods Hole species in the vicinity of Plymouth than the 15 per cent which have been recorded. To what degree these differences in fauna are due to differences in physical conditions

[a] We fear that much ingenuity has been wasted in the past in an endeavor to distinguish all the various "faunas" represented on a single section of our coast. Such entities are, after all, to a large extent figments of the imagination.

and to what degree they are due to geographical isolation we can not say. The surface temperature of the sea in the neighborhood of Plymouth is said to range from about 44° F. (February) to about 59° F. (August). (See Dickson, 1892, p. 276.) In this respect the conditions are far different from those in Vineyard Sound, in which the annual range of temperature is roughly from 30° F., or less, to 70°. On the other hand, we know that broad expanses of ocean are effective barriers to distribution, even for marine organisms.

Although we have not undertaken the ambitious task of making extended comparisons between the Woods Hole fauna and the faunas of other sections of the Atlantic coast, we have nevertheless been able to give some answer to the questions: (1) Have the majority of our more representative species a range which is predominantly northward or one which is predominantly southward? (2) In how large a degree is Cape Cod a barrier to distribution?

As stated above, we have considered for this purpose only those species which have been taken at 10 or more of our dredging stations, and which, therefore, may be regarded as those which are most truly representative of our local benthos. Of such species there are 202, excluding 9 species of Protozoa. In the various sections of chapter IV these species have been grouped according to their range upon our coast, and a synopsis of these separate lists is presented in a table herewith. It may be repeated that a species has been regarded as predominantly northward-ranging, whose range (in latitude) to the northward on our coast is at least twice as great as its range to the southward.[a] A species has been regarded as southward-ranging which presents the converse type of distribution. The column headed "Equal" refers to those species whose known range in one direction does not greatly exceed the known range in the other direction; while the doubtful column includes those concerning which our data are insufficient. In many cases they have been found only in the immediate vicinity of Woods Hole.

	Predominantly northern.	Predominantly southern.	Equal.	Doubtful.	Total.	Known to occur north of Cape Cod.	Known to occur south of Woods Hole region.[b]
Sponges	1	1	1		3	2	2
Cœlenterates	6	3	2	2	13	11	9
Bryozoa	4	4	7	6	21	12	11
Echinoderms	3	2		2	7	6	7
Annulata	5	22	2	1	30	13	27
Sipunculida			1		1	1	1
Cirripedia		1			1	1	1
Amphipods	7	5		7	19	8	6
Isopods		2	1		3	1	3
Decapods	2	8	3		13	8	13
Pycnogonids		1		1	2	1	1
Mollusks	16	43	8	1	68	50	67
Tunicates		4		4	8	3	5
Fishes	2	5	6		13	13	12
Total	46	101	31	24	202	130	165

[a] This criterion has not been applied to those cases in which it is definitely known that the extreme southern records relate only to great depths.

[b] Long Island Sound has not been regarded as south of the Woods Hole region. Had it been so considered, the figures in this column would have been materially increased.

Of the entire 202 species, 101, or exactly 50 per cent, are believed to have a range upon our coast which is predominantly southward; 46 species (23 per cent) have a range which is predominantly northward; while 31 of them (15 per cent) have a range of approximately equal extent, so far as known, in both directions. The remaining 24 species have been relegated to the doubtful column. The fact to be emphasized is that the ratio of southward-ranging species (as thus defined) to northward-ranging species is greater than two to one, while about 15 per cent of them do not seem to be thus restricted in latitude.[a]

Viewing these 202 species in another way, it is to be noted that 130, or about 64 per cent of them, are known to have a range extending north of Cape Cod, leaving 72 of them (36 per cent) which, so far as reported, have not transcended this barrier. Doubtless more complete information will reduce the latter figure. As has already been pointed out, any locality where extensive collecting has been done is sure to figure as the reputed limit of distribution, whether northern or southern, for many species. It is significant, therefore, that only 37 of the species under consideration (18 per cent) have not yet been recorded from points south of Woods Hole.[b] Comparing this figure with the 36 per cent which are not known to occur north of Cape Cod, it may be that we have some measure of the real effectiveness of the last as a barrier to distribution.

Crude, in the extreme, as any such computations must be, the conclusions seem to be fairly well grounded (1) that Cape Cod does have an appreciable influence as a barrier to distribution, and (2) that the southern types preponderate considerably over the northern ones in our Woods Hole fauna, or at least in that part of it which is accessible to the dredge. These generalizations may not be true of each individual group (e. g., cœlenterates and amphipods); and in general it must be remembered that a considerable minority of northern forms are included in our local fauna, while about 64 per cent of our species are known to occur north of Cape Cod. On the other hand, it is well to state that our local fish fauna, which is but sparingly represented in our dredging records, and consequently plays little part in the foregoing tabulation, is overwhelmingly southern, 75 per cent being southward-ranging in the foregoing sense of the term, while nearly 50 per cent of the total number of recorded species are such as are reputed to find in Cape Cod their northern limit of distribution. And, lastly, we must bear in mind that we are here dealing only with the benthos of the region, the plankton, as well as the littoral fauna, being left out of consideration.

6. COMPARATIVE DISTRIBUTIONS OF CLOSELY RELATED SPECIES.

Turning to another phase of our subject, it would be unreasonable to look to the results of such a survey as the present one for any considerable light upon the origin of species. Those who insist upon the importance of isolation as a factor in species differentiation are wont to maintain that different subspecies do not coincide in their ranges, but that these supposedly incipient species are practically always separated from one another, geographically or otherwise. After the complete splitting of a species, i. e., its replacement by several specifically distinct forms, these latter may by migration, it is said, come to occupy the same territory. .

[a] The similar treatment by Hoyle of the deep-water fauna of the Clyde sea-area was unknown to the present writers at the time when the foregoing discussion was written. (See Hoyle, 1890, p. 463 et seq.).

[b] More strictly, south of Vineyard Sound and Buzzards Bay. Block Island and Long Island Sound have not been regarded as farther south.

Jordan, who is one of the foremost recent advocates of the theory of evolution by isolation, tells us (1905) that "it is extremely rare to find two subspecies inhabiting or breeding in exactly the same region." Again: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort" (p. 547). This, he says, "may be raised to the dignity of a general law of distribution."

Few groups of marine animals have been worked as intensively as have the birds and fresh-water fishes upon which Jordan chiefly relies for evidence in favor of his theory. It is largely due to this fact, probably, that "subspecies," "varieties," and "geographical races" play a relatively minor part in the taxonomy of marine animals. We thus have practically no data at our present disposal to test the first of Jordan's assertions quoted above. A case which perhaps deserves mention at this point, though its relevance may well be questioned, is that of the mollusk *Polynices heros*, and its supposed variety, *triseriata*. We must make the reservation at once that these are regarded by some conchologists, e. g., Dall, as distinct species, and in fact we have ourselves followed Dall in so listing them in our catalogue.[a] A glance at the charts[b] (187,188) reveals the fact that while the two forms coexist throughout much of their range, they nevertheless do not present the same distribution patterns, but appear to show distinct preferences as to habitat. There is, however, no real *geographical* isolation, for the two forms occur on closely adjacent parts of the sea floor, being taken together, not infrequently, in a single dredge haul.[c] Whether or not these two species (or varieties?) cross freely, and with what results, we have no means of knowing at present.

It is impossible, likewise, for us to state whether or not the species *nearest related* to any given one among our local fauna occurs in this region, or in a "neighboring district." Such a question could be answered only after an exhaustive research into the fauna of neighboring parts of our coast. We have a considerable collection of data, however, with which to answer the kindred questions: (1) To what extent do members of the same genus tend to differ in habitat? and (2) Are different members of the same genus less likely to be associated together than species not so closely related?

As bearing upon the first of these questions, the comparative distributions of different species of the same genus have been presented by us in a large number of cases. The reader is especially referred to the following examples:

Eudendrium, 2 species (charts 16, 17).
Tubularia, 2 species (charts 18, 19).
Asterias, 2 species (charts 48, 49).
Nephthys, 2 species (charts 57, 58).
Ampelisca, 2 species (charts 87, 88).
Pagurus, 4 species (charts 109–112).
Cancer, 2 species (charts 115, 116).
Anomia, 2 species (charts 123, 124).
Pecten, 2 species (charts 125, 126).
Arca, 3 species (charts 131–133).
Astarte, 2 species (charts 138, 139).
Busycon, 2 species (charts 164, 165).
Crepidula, 3 species (charts 183–185).
Polynices, 3 species (charts 186–188).
Amaroucium, 3 species[d] (charts 195–197).

[a] In any case the relationship will be conceded as being very close.

[b] Only the occurrence of living specimens (designated by circles) can be taken into account here, since the dead shells are probably transported considerable distances by hermit crabs.

[c] As regards geographical range, that of *Polynices heros* is stated by Dall as extending from Labrador to Virginia; that of *triseriata* being practically identical, i. e., from Labrador to Cape Hatteras.

[d] In our catalogue we have followed Dr. Van Name in not regarding one of these as a distinct species.

There are several ways in which two species may differ in respect to their distribution patterns: (1) The species may occur throughout practically the same area, differing only in their relative abundance; (2) the range of one may be restricted to a portion of the area occupied by another; (3) they may have distributions which are in a certain degree complementary to one another.

Referring to the genera named, it will be found that in few cases, if any, are the distributions of two members of the same genus practically identical, both as regards the area inhabited and the frequency of occurrence. In a number of instances, however, they differ only in respect to frequency.

The type of difference most often realized upon our charts is the second among those mentioned above. In such cases one species may occur throughout only a portion of the territory occupied by the other; or, at least, it may not be well established except in this portion.

The third condition—that of two species of the same genus having distribution patterns which are complementary to one another—is realized in a surprisingly small number of cases upon our charts. It appears most clearly from a comparison of the distributions of *Pagurus acadianus* (chart 110) and *P. annulipes* (chart 112). We have seen that these are respectively northward-ranging and southward-ranging species; so that the habitat selected by each in local waters is not improbably determined by temperature.

It is a familiar fact to field naturalists that the various members of the same genus frequently, if not generally, occupy somewhat different habitats. Obvious instances of this are not uncommon among our local littoral and shallow-water fauna, as for example the three familiar species of the genus *Littorina*. Now, our dredging charts are not adapted to revealing such slight differences of habitat as may occur within the limits of a single "station." In the charts for *Crepidula*, for example, there is nothing to show that *C. fornicata* does not coincide in its habitat as well as its distribution, with *C. plana*; whereas we know that, in most cases, the latter occupies the inside of a hermit-crab shell, while the former may occupy the outside of the same shell, or may adhere to any solid object whatever. It is probable, likewise, that the drifting of shells and other lifeless remains may result in an apparent obliteration of actual distinctions in the distribution of species. Finally, it seems needless to remark that in no single case is the entire range of a species indicated upon one of our charts. Thus, even in cases where two species appear to coincide in their distribution locally, the range of one may extend into far deeper water, off the coast, than that of the other. It seems to us, therefore, that the differences in the distribution of closely related species have been minimized, rather than exaggerated, in our graphic representations.

Whether or not specific differentiation preceded or followed these changes of habitat, or whether they went on *pari passu* with such changes, is not even suggested by any of the facts which we have encountered. Who can say, for example, whether the tendency to restrict itself to muddy bottoms preceded or followed the differentiation of the amphipod *Ampelisca macrocephala* as a species distinct from *A. spinipes*? Nevertheless, the bare fact that various closely related species do show decidedly different distribution patterns is one of great interest, for it shows that the slight morphological differences by which the species are distinguished from one another are oftentimes correlated, with marked physiological differences sufficient to adapt the two to differing habitats. Thus the assertion so often made that the slight structural differences by which we distinguish one species from another are commonly of no conceivable utility, and therefore can never have arisen through the action of natural selection, loses much of its force. While it may be true that these slight structural differences in themselves can play no significant rôle in the life of the organisms concerned, it is likewise evident that there are certain correlative physiological changes sufficient to adapt the organisms to somewhat different modes of existence. That natural selection has been the controlling factor in the origination and perpetuation of such specific differences, whether morphological or physiological, is far from certain. But that the characters concerned are in most cases too insignificant to be of selective value is also far from certain.

Where we have to do merely with the adoption of a more restricted habitat by one species than by another, it is quite possible that the physiological difference in question relates merely to general constitutional vigor; i. e., the less hardy species may restrict itself to the more favorable portion of the habitat.[a] Where, however, the ranges of the two species are more or less complementary to one another, particularly if they do not coincide throughout any portion of their extent, such an explanation is of course out of question, and we are obliged to fall back upon the assumption that each is more or less specifically adapted to its respective habitat.

In order to throw light upon the second of the above questions (i. e., Are members of the same genus less likely to be associated together than species which are not so closely related?), we have adopted a method employed by Herdman (1895). This author, after noting the relatively large number of genera represented by the species taken in a single dredge haul,[b] writes: "These figures are particularly interesting in their bearing on the Darwinian principle that an aminal's most potent enemies are its own close allies. Is it then the case, as the above cited instances suggest, that the species of a genus rarely live together; that if in a haul you get half a dozen species of lamellibranchs, amphipods, or annelids they will probably belong to as many genera, and if these genera contain other British species these will probably occur in some other locality, perhaps on a different bottom, or at another depth? It is obviously necessary to count the total number of genera and species of the groups in the local fauna, as known, and compare these with the numbers obtained in particular hauls." In Liverpool Bay, for example, "the known number of species of higher Crustacea is 90, and these fall into 60 genera. So the genera are to the species as 2 to 3," whereas in certain dredging collections cited "the genera are to the species on the average about as 28 to 31, or nearly 7 to 8. Again, the total number of species of Tunicata is 46, and these are referred to 20 genera; while in the case given above * * * the 12 species taken on one spot represented 10 genera, or a little over a quarter of the species represented half the genera. These, and many other cases which we might quote, seem to show that a disproportionately large number of genera is represented by the assemblage of species at one spot, which means that closely related species are, as a rule, not found together" (p. 463).

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[a] This suggestion has been made to us by Prof. Herdman.

[b] This fact was pointed out by Sir John Murray (Challenger "Summary," p. 1435), who, however, restricts its application to great depths, concluding "in the deepest zone, therefore, the species stand to the genera in the ratio of 5 to 4, and in the shallowest zone nearly as 3 to 1."

When subjected to statistical analysis, our results are in full agreement with those of Herdman, though we are not convinced of the truth of his interpretation.

As shown in the table on page 77, the average number of species per dredge haul, as based upon the 458 regular stations of the Survey, is 37.0, while the average number of genera per dredge haul is 34.3. Thus the average number of species per genus is approximately 1.08,[a] or the ratio of species to genera is about 13 to 12. This ratio we have thought best to compare, not with that derived from a consideration of the entire array of species and genera for the Woods Hole Region, but with that based upon the total number of species and genera, so far as encountered by us in the dredge. Among these are included 510 determined species, representing 361 genera. The average number of species per genus is thus approximately 1.41, or the ratio of species to genera is as 7 to 5.

So far, then, we seem to be in complete agreement with Herdman. A quite different explanation from that given by him has, however, suggested itself. It has occurred to us that the same relations would follow if some of our genera contained a considerable number of uncommon species. These latter might not be taken with sufficient frequency to affect appreciably the average number of species per dredge haul, but they would greatly augment the number of species per genus when the total number of those encountered were taken into account. Now, as a matter of fact, many of the genera do contain a considerable number of rare species—species which were taken once only, or a very few times—in addition to common ones. On the other hand, it is true that we also meet with certain rare species which are the only representatives in local waters of their respective genera. Thus there would seem to be nothing to show whether the inclusion of these less common species would augment or decrease the average number of species per genus in our fauna.

One test may be applied, however. We may restrict our computation to the *commoner* species, and determine the ratio of species to genera among these. For this purpose let us employ those species which were taken at 10 or more of our dredging stations. Among these we find 209 species[b] representing 178 genera. The average number of species per genus is thus about 1.18, a figure very much smaller than that representing the number of species per genus in the entire array of organisms dredged by us. Indeed it approaches more nearly the figure (1.08) expressing the average ratio within the limits of a single dredge haul. Thus the conclusion seems warranted that the larger number of species per genus found to occur in the fauna at large, as compared with the average number for a single dredge haul, is due largely, if not wholly, to the inclusion in the former reckoning of the rarer members of certain genera. Such species do not, on the other hand, occur with sufficient frequency to appreciably affect the ratio for the average dredge haul. If this reasoning be correct, what seemed to be a fascinating and clear-cut demonstration of a significant principle of distribution falls to the ground.

[a] We are quite aware that the ratio between these gross averages has not exactly the same value as the average of the separate ratios for the various dredge hauls. In other words, $\frac{a+b+c}{3} \div \frac{x+y+z}{3}$ has not the same value as $\left(\frac{a}{x}+\frac{b}{y}+\frac{c}{z}\right) \div 3$. Where the number of terms is so great, however, the results derived from the two methods of computation must be sufficiently close for present purposes.

[b] Including Protozoa.

7. CHANGES IN THE COMPOSITION OF THE LOCAL FAUNA.

Every area of land or sea doubtless undergoes more or less frequent changes in the composition of its fauna and flora, due to the immigration or artificial introduction of exotic species or the extinction of indigenous ones. For the Woods Hole region we have certain well-known and highly authentic instances of this phenomenon, together with some others which seem probable, if only inferential.

The best-known local instances of the sort are those of the European periwinkle, *Littorina litorea*, and of the small sea anemone, *Sagartia luciæ*. Rather full accounts of the history of both of these immigrants are fortunately extant. (See Verrill, 1880; Ganong, 1886; Verrill, 1898; Parker, 1902. These accounts are summarized in our own catalogue.) It may be here remarked that the periwinkle reached Woods Hole from the north about 1876; while the anemone seems to have come from the south, arriving about 1898. Within about 30 years, and perhaps much less, *Littorina litorea* has become the most abundant and generally distributed of our littoral (intertidal) mollusks, while *Sagartia luciæ* in a considerably shorter time has become by far the commonest local actinian. It would be interesting to know what effects, if any, these immigrants have had in limiting the abundance or restricting the distribution of species already present. Unfortunately few observations, if any, have been made to test this point.

Concerning certain other species, we have some reasons for believing either that they are, in local waters, far more abundant now than formerly, or that they have actually migrated hither within recent years. The only other alternative seems to be that they were overlooked or confused with quite distinct species by a number of competent naturalists. For example, of our four local species of hermit crabs, *Pagurus annulipes* is second in abundance only to the ubiquitous *P. longicarpus*. Its distribution in local waters is almost universal, as will be seen from a glance at the distribution chart for this species. Yet this hermit crab was not mentioned by Verrill and Smith in 1873,[a] nor, so far as we are aware, has it been recorded for local waters in any work prior to Miss Rathbun's catalogue of the Crustacea of New England (1905). We have, it is true, learned from Miss Rathbun that specimens of this crustacean were recently found among the earlier material dredged by Verrill and Smith. But the fact that it was overlooked, or at least not mentioned by these writers, raises strong doubts as to whether it occurred then in its present abundance.

Another problematic case is that of one of the shore barnacles, *Chthamalus stellatus*,[b] which at present is extremely abundant upon stones and boulders between tides everywhere. This well-known European species is, in our waters, at least, quite distinct in appearance from the other common shore barnacle (*Balanus balanoides*). Yet it has not been mentioned in any catalogue of New England fauna, although several far less common cirripedes have been listed. It is hard to believe that this species has been habitually confused with *Balanus balanoides* by the long succession of field naturalists and systematic zoologists who have exploited the shores of New England for

[a] Allowance must be made for the fact that, in the words of one familiar with the circumstances, "the Vineyard Sound report was prepared when the Fish Commission had spent but one summer at Woods Hole, and was rushed through expeditiously for insertion in the Fish Commission Report for 1871–72. It did not list everything that had been discovered, but omitted much that had not been sufficiently studied."

[b] For an account of this case, see Sumner, 1909.

over a century.[a] These men erred rather in the direction of discovering too many new species than in ignoring well-established ones.

The medusa, *Gonionemus murbachii*, does not seem to have been observed until 1894, when according to Perkins (1902) it "made an astonishingly sudden appearance upon the scene." Yet at present this relatively conspicuous and readily recognizable medusa is one of the most familiar objects of research in the Woods Hole laboratories. Its distribution, locally, appears to be rather restricted, however, most of the collecting for this species being carried on in one small salt-water pond.

The large noncolonial hydroid, *Tubularia couthouyi*, whose conspicuous yellow perisarcs are dredged with considerable frequency in Vineyard Sound, was likewise not referred to in the report of Verrill and Smith, although this latter listed a number of other hydroids which have not been noted by any subsequent observers. And it is likewise somewhat astonishing that neither of our local species of *Arenicola* was mentioned in the Vineyard Sound report, although one, at least, of these immense annelids is now common at points in the vicinity of Woods Hole.

We can not attribute so much importance to the failure of previous writers to record the gastropod *Lacuna puteola*, since this species, although very abundant, is likewise very small. The same may be said of a considerable number of other species which are comprised in our list but were not recorded by various previous observers. Inconspicuous or uncommon species may readily be overlooked, even by competent collectors. Such an oversight seems unlikely, however, in the case of the other examples cited above.

Just the opposite state of affairs is to be noted in the case of certain species which were recorded by Verrill as common in local waters, but which the present writers have seldom or never met with. As a striking instance of this is to be mentioned the anemone *Edwardsia lineata* Verrill, concerning which the last-named zoologist makes the following entry (p. 739): "Vineyard Sound and off Gay Head, 6 to 12 fathoms, among ascidians, annelid tubes, etc., abundant." A search in just such situations, both by Prof. Hargitt and by ourselves, has failed to disclose a single specimen. The size, as stated by Verrill (25-35 mm. long), makes it unlikely that the species has been persistently overlooked by us.

The barnacle *Balanus crenatus* was recorded by Verrill and Smith as "dredged abundantly in Vineyard Sound." While we have found it to be common upon piles at Vineyard Haven, we have never, with a few possible exceptions, encountered this species with the dredge, either in Vineyard Sound or Buzzards Bay. This is true despite the fact that practically all of the barnacles dredged by us were saved for subsequent inspection.

The crabs *Libinia dubia* and *Panopeus* [*Eurypanopeus*] *depressus* are of far less general occurrence in these waters than the statements of Verrill and Smith seem to imply. Although we have encountered both of these species in the shallow waters near shore, we have not a single authentic record of either species having been taken in the dredge during the course of our operations.

While it is not likely that all of these discrepancies between earlier and later statements can be attributed to actual changes in the occurrence of species, it is probable that some of them are due to such changes.

[a] It has just been learned from Prof. M. A. Bigelow that he noted the occurrence of this barnacle at Woods Hole in 1898.

8. CONCLUSION.

To the reader who would demand an exact economic equivalent for the labor and money here expended, our answer must be a very general one. Science and industry move together. Industry is helpless without the aid of science, and the greatest industrial progress is at present being made by those countries which realize this fact most fully. But science can never prosper if forced to play the rôle of a servant. She must be free to pursue her own ends without being halted at every step by the challenge: *Cui bono?* The attempt to restrict our scientific experts to problems of obvious economic importance would be equivalent to depriving ourselves of their services altogether. It is to-day accepted as a commonplace that all the great discoveries of a practical nature have rested ultimately upon principles first brought to light by the seeker after truth. The enlightened manufacturer of Germany looks upon a well-paid scientific investigator as a good invesment. As a result of this policy the rest of the world is looking on uneasily, while its own industries pass into the hands of this farsighted competitor. Great Britain and the Scandinavian countries, the great fishing nations of Europe, have long been leaders in the scientific investigation of the sea. And in recent years we have witnessed the formation of an international council, representing all of those nations having an immediate interest in the fisheries of the North Sea, and organized for the study of hydrographic and biological problems as well as of purely economic ones. To Americans there should be no novelty in all this. Let us keep in mind the oft-quoted words of the distinguished founder of our Fish Commission in outlining the policy adopted by him:

> As the history of the fishes themselves would not be complete without a thorough knowledge of their associates in the sea, especially such as prey upon them or in turn constitute their food, it was considered necessary to prosecute searching inquiries on these points, especially as one supposed cause of the diminution of the fishes was the alleged decrease or displacement of the objects upon which they subsist.
>
> Furthermore, it was thought likely that peculiarities in the temperature of the water at different depths, its chemical constitution, the percentage of carbonic-acid gas and of ordinary air, its currents, etc., might all bear an important part in the general sum of influences upon the fisheries; and the inquiry, therefore, ultimately resolved itself into an investigation of the chemical and physical character of the water, and of the natural history of its inhabitants, whether animal or vegetable. It was considered expedient to omit nothing, however trivial or obscure, that might tend to throw light upon the subject of inquiry, especially as without such exhaustive investigation it would be impossible to determine what were the agencies which exercised the predominant influences upon the economy of the fisheries.

So that if we can not, from our present labors, offer any suggestions of direct value to the practical fisherman, we trust that we have at least added to the intelligent understanding of the marine life of our coast. And we likewise trust that the *ultimate* benefit to the practical fisherman will be as great as that to the man of science.